

Figure 6

Cross section of an egg capsule from *Nerita funiculata*. hl, homogenous inner layer; ml, outer mucous layer; oa, fertilized eggs; s, spherulites.

STARMÜHLNER (1976, 1983) also noted that the reproductive systems of *Neritilia* are not as complex as those in other neritids. Species in this genus are lacking both the ductus enigmaticus and the duct that joins the receptaculum seminis to the sperm duct. In addition, the spermatophore sac is a simple elongated pouch. Moreover, *Neritilia* is usually placed in a separate subfamily of the Neritidae.

Curiously, neither a crystal sac nor a separate penis was observed in *Titiscania*. In an earlier study on *T. limacina*, MARCUS & MARCUS (1967) observed a small empty sac attached to the anterior end of the pallial oviduct. Because no spawning was observed, it was only speculated that the sac functioned as a crystal or reinforcement sac. In addition, they mentioned the presence of multiple copulatory bursae in the female. These structures were not observed in specimens during my study. Unfortunately only females were collected during their study so the male genital tract was not described. Further anatomical work needs to be done on the anatomy of *Titiscania* to clarify its systematic position among the Neritimorpha. Presently the genus is placed in its own family. For the family Neritidae, the presence of a crystal sac appears to be an autapomorphic character.

ANDREWS (1937) described the spermatophores from several species of neritids and noted a wide variability in form, including the length of the spermatophoric filament. She also mentioned that these filaments serve as conduits for sperm transfer to the receptaculum seminis. This, however, contrasts with the finding by FRETTER (1984) for *Phenacolepas*. Here the sperm are liberated from the spermatophores directly into the lumen of the bursa or spermatophore sac. Moreover, there appears to be a relationship between the filament length and the nature of the duct to the receptaculum seminis. In *Nerita* and *Theodoxus* the spermatophoric filaments are longer than those found in *Neritina* or *Titiscania*. The same holds true for the duct joining the receptaculum seminis to the spermatophore sac or, as in *Theodoxus*, to the albumin gland.

From the examination of stained sections and ciliary currents within the genitalia of *Nerita funiculata*, the following sequence of events during and after mating can be inferred. During copulation the spermatophores enter the

genital opening and are moved by peristalsis up the sperm duct and stored in the spermatophore sac. Stained sections reveal spermatophoric filaments in the lumen of the duct that leads to the receptaculum seminis. Hence, the spermatozoa apparently travel to the receptaculum through these filaments. This has been suggested for other species of neritids (ANDREWS, 1937; BERRY *et al.*, 1973). As was previously mentioned, the sperm are then stored in the receptaculum until they are utilized for fertilization. The empty spermatophores appear to be ingested by the epithelial cells that line the wall of the spermatophore sac. Sections reveal left-over fragments surrounded by secretory droplets. The ova travel down the oviduct and enter the fertilization chamber by way of the ventral ciliated groove. Here they are apparently fertilized by sperm released from the receptaculum. These fertilized eggs then pass through and are mixed with secretions from the albumin glands. Anteriorly they enter and pass through the capsule gland where they become coated with secretions produced by the subepithelial gland cells in this region. These secretions constitute the egg capsule, which hardens when it passes through the nidamental opening to the outside.

In many species of neritids the walls of egg capsules are reinforced by inorganic particles (ANDREWS, 1933, 1935; FRETTER, 1946). Moreover, these reinforcements consist of different substances. In *Nerita*, for example, these particles are spherulites consisting primarily of calcium carbonate. According to ANDREWS (1935) they are apparently synthesized in the digestive gland. There is, however, no evidence of spherulite formation in the digestive glands of the neritids in this study. Since both *Nerita funiculata* and *Nerita scabricosta* live on limestone reefs, it is possible that minute particles of lime are scraped up along with the food by the radula. As they pass through the gut they are modified and become spherical. For *Neritina* and *Theodoxus* the egg capsules are impregnated mostly with sand. However, diatom skeletons and sponge spicules also occur in the capsules of these genera (ANDREWS, 1935). No spawn was observed for *Titiscania*.

The present study gives the first evidence of a sorting mechanism in the crystal sac of *Nerita*. A possible advantage in using similar size particles to reinforce and harden the capsule wall would be to provide a relatively smooth

surface to minimize the effects of waves and currents. There is no evidence of sorting mechanisms in the crystal sacs of *Theodoxus* or *Neritina*. Because these species use primarily sand to strengthen their egg capsules, a sorting would not be needed, as sand is usually already sorted by currents and waves. However, more work is needed to clarify this and other issues, such as the exact site of fertilization and the mechanism by which spermatophores are transferred from male to female.

Until recently the Neritimorpha were considered to be intermediate between the Archaeogastropoda and the Caenogastropoda because of their shared characters with the latter group (BOURNE, 1908; FRETTER, 1965, 1984). However, HASZPRUNAR (1988) has provided strong arguments for placing the Neritimorpha lineage even before the Vetigastropoda. This is based in part on previous studies concerning their special mode of shell formation, discussed by THOMPSON (1980), and differences in their sperm morphology (HEALY, 1988). If HASZPRUNAR (1988) is correct, the advanced characters exhibited by neritimorphs, including those of their genitalia, arose several times and can be considered convergences.

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Indirect Evidence of a Morphological Response in the Radula of *Placida dendritica* (Alder & Hancock, 1843) (Opisthobranchia: Ascoglossa/Sacoglossa) to Different Algal Prey

by

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Abstract. Examination of radulae from the ascoglossan mollusk *Placida dendritica* (Alder & Hancock, 1843) collected in New Zealand, Australia, Japan, and west coast North America revealed two morphological types. Each was correlated with the type of alga from which the slugs were collected. Those feeding on perennial *Codium* had smaller teeth, more teeth, and a tight radular coil in an enlarged ascus. Those feeding on seasonal *Bryopsis* and *Derbesia* had larger teeth, fewer teeth, and only a slightly curved radular ribbon (never a coil) in the ascus. This apparent morphometric response of radular structure to algal structure and defenses may explain similar sporadic size discrepancies observed in populations of three other ascoglossan genera, *Alderia*, *Elysia*, and *Limapontia*.

INTRODUCTION

For several species of ascoglossans, the radular teeth can, numerically and morphologically, (1) vary ontogenetically within an individual; (2) vary seasonally within one species; (3) have a reversal of the normal process of producing sequentially larger teeth; and (4) vary in the rate of tooth production as determined by comparing body lengths to the total number of teeth (RAYMOND & BLEAKNEY, 1987; BLEAKNEY, 1988). This paper reports a fifth category that had not previously been suspected, namely that the size of and production rate of teeth can vary in response to the type of algae eaten. Presumably this is a response to the degree of mechanical difficulty in penetrating algal filaments and to the effort required to suck out the cell sap.

BLEAKNEY (1989) recently demonstrated consistency over much of the Pacific Basin in the ultrastructure of the cutting edge of teeth of *Placida dendritica*. However, he noted in particular a perplexing lack of direct relationship between body size and total number of teeth. In most cases the largest animals, 14–20 mm in length, had fewer teeth than many animals only 3–4 mm in length. He concluded that this discrepancy was a reflection of either long geographic isolation and had a genetic basis, or was merely a temporal extreme such as he had observed in Nova Scotia populations of *Elysia chlorotica* Gould, 1870 (RAYMOND &

BLEAKNEY, 1987). However, after examining a series of *P. dendritica* from Oregon, a third and more plausible explanation is now available.

MATERIALS

Dr. Cynthia Trowbridge sent me three separate lots of *Placida dendritica* collected from three species of alga—*Codium fragile* (Suringar) Hariot, *Codium setchellii* Gardner, and *Bryopsis corticulans* Setchell—in the hopes that I might discover radular differences. She felt that differences in the general appearance and behavior of *Placida* on these algae indicated possible specialization and speciation. However, and without exception (based on examination of 10 slugs from each alga), the pronounced morphological variation observed fell into only two categories and these were directly correlated with the two genera of algae. These observations prompted a re-examination of my notes and collections of *P. dendritica* from British Columbia, Japan, Australia, and New Zealand, and some of those data are included in Figure 1.

RESULTS

In every case, the largest animals had been collected from *Bryopsis* or the related genus *Derbesia*. The radular ribbon

of *Bryopsis*-feeding *Placida dendritica* had fewer but much larger teeth and a slightly curved, descending radular limb (Figures 2, 3). In sharp contrast, slugs from *Codium* had many more teeth but much smaller ones (Figures 4, 5) and their strongly coiled descending radular limbs were already evident at body lengths of only 3 and 4 mm. Even with body lengths of 14 mm, slugs from *Bryopsis* had only a slightly curved ribbon in the ascus area.

Figures 2 to 5 are of two equally large buccal masses from two 8 mm *Placida dendritica*, photographed at the same magnification, yet the tooth bases in the ascending series of the *Bryopsis* feeder are at least twice as large as the *Codium* example. The differences in the size and number of teeth do not seem to effect the relative size of the buccal mass in the two categories, although a larger sample might emphasize an incipient divergence indicated by query arrows in Figure 6. The numerous additional teeth produced by the *Codium*-feeding slugs are accommodated outside the buccal mass within an enlarged ascus area.

DISCUSSION

Available morphological information indicates that *Placida dendritica* is a single species, at least within the Pacific Basin (BLEAKNEY, 1989). Among the three collections from Oregon, there were no differences in the ultrastructure of the serrated edge of the radular teeth. If *P. dendritica* actually consisted of a *Codium*-species and a *Bryopsis*-species, one would expect real differences in the teeth reflecting the considerable differences in structure of the two algae. The only radular differences detected were the relative size of teeth and the total number of teeth, two variables common to any population. That these two variables, as well as the category of maximum body size, were directly related to the different algal prey is significant. That the two algal genera were *Codium* and *Bryopsis* is equally significant for the former is perennial (pseudoperennial) and the latter highly seasonal. Perennial or pseudoperennial plants should (as predicted by evolutionary theory) partition more resources into anti-herbivore defenses. This becomes manifest as degrees of edibility and digestability, and ultimately affects the growth rates of predators. CLARK & DEFRESE (1987) emphasized the strong evolutionary interplay of algal life histories, physiology, and structure with that of alga-sap-sucking ascoglossans.

Because *Codium* is a perennial, it undoubtedly has developed defenses to reduce grazing efforts of ascoglossans, which are generally directed at the coenocytic filaments of siphonaceous algae because one puncture by a radular tooth gains access to the entire thallus system. Access to *Codium* must be frustrated in part by its peculiar surface which consists of a carpet of erect, compacted, clavate, utricles whose exposed apices are capped by a lamellate cuticle (WOMERSLEY, 1984). These utricle subunits almost amount to a septate condition, as the feeding slug must shift from one utricle to another to extract sap. Narrow radular teeth may be more effective than stout ones in penetrating this armor, but at the same time, under this

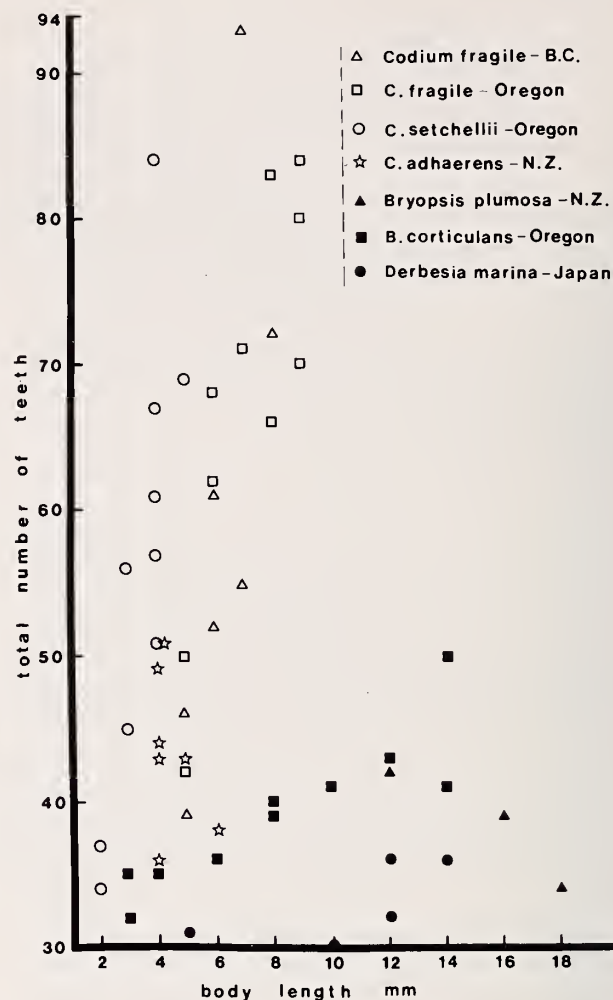


Figure 1

Relationship of body length and total number of teeth of *Placida dendritica* from various geographic regions to type of alga fed upon. *Codium* species are plotted as open symbols, and *Bryopsis*/*Derbesia* are solid symbols.

repetitious puncturing of numerous utricles, the serrations may wear down faster and tips break off and pieces chip out (see photographs in BLEAKNEY, 1989).

The life history of *Bryopsis*, in contrast, involves a seasonal appearance of irruptive, transient populations with little necessity to evolve major protective toxins or mechanical barriers. The thin-walled, plumose thallus of *Bryopsis* may be most effectively penetrated and split open by a large diameter tooth, and certainly the amount of cell sap extracted per puncture must be far greater from *Bryopsis* than from *Codium*. The nutrient value is probably far higher as well, for as CLARK & DEFRESE (1987) pointed out, perennial algae tend to produce a spectrum of secondary metabolites whose toxic effects are not necessarily direct, but which may serve the alga by inhibiting (or slowing) growth and reproductive processes in the attacking ascoglossans.



Explanation of Figures 2 to 5

Figures 2, 3. Entire buccal mass and enlargement of the radular area of an 8-mm-long *Placida dendritica* found on *Bryopsis corticulans* in Oregon, July 1988. Scale bar = 80 μm .

Figures 4, 5. Entire buccal mass and enlargement of the radular area of 8-mm-long *Placida dendritica* found on *Codium fragile* in Oregon, July 1988. Scale bar = 80 μm .